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Treeline composition and biodiversity change on the southeastern Tibetan Plateau during the past millennium, inferred from a high-resolution alpine pollen record

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ABSTRACT

Climate variability has been impacting the terrestrial ecosystems. However, some important processes relating to the response of vegetation to climate change in alpine regions, such as treeline composition and associated plant diversity change, have not been well understood in terms of multi-centennial scales. Here, we present a well-dated high-resolution palynological record from Basomtso, southeastern Tibetan Plateau (TP), to discuss the vegetation change and the relevant climate forcing. Our results manifest that the treeline position, composition and plant diversity around Basomtso did change greatly during the past millennium. The cold events (*ca.* 720-650 cal yr BP and *ca.* 400-50 cal yr BP) were considered crucial to force these changes. Cold temperature limited the growth of trees in the high elevations and thus led to downslope movement of treeline and conspicuous decrease of dominant tree species. Space and resource released from the upper forest triggered shrub and herb taxa expanded to lower elevations and even new species can dispersed to this area and survived, leading to changes in vegetation composition and diversity. Although the climate warming is pronounced since the 20th century, treeline distribution, vegetation composition and species diversity seem have not been recovered from the previous cold period. And the vegetation succession in the mountains of the southeastern TP will probably develop slowly in the coming decades. Our results highlight the need for long-term climate and vegetation monitoring and analysis in order to better understand the regional dynamics of treeline movement and plant diversity change during climate transition period.

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1. Introduction

Climate change has a great impact on the terrestrial ecosystem, including the shifts of treeline position (Harsch et al., 2009) and the changes in plant diversity (Klein et al., 2004; Pauli et al., 2012). And this impact is especially obvious in high elevations (Colombaroli and Tinner, 2013; Harsch et al., 2009; Liang et al., 2016; Pauli et al., 2012). As climate warming has been very pronounced at high altitudes and latitudes (Beniston et al., 1997), studies about the response of vegetation to climate change at alpine areas, i.e., the changes of treeline position, composition and plant diversity, have therefore gained extensive academic attentions (Birks et al., 2016a; Chen et al., 2011; Cotto et al., 2017; Liang et al., 2016; Olsen and Klanderud, 2014; Pauli et al., 2012; Wielgolaski et al., 2017).

Alpine treeline is assumed to be temperature sensitive (Paulsen and Körner, 2014). It is expected to respond to recent climate warming by advancing beyond their current position and/or with changing physiognomic structure and biodiversity (Harsch et al., 2009; Liang et al., 2011, 2016; Wielgolaski et al., 2017). An upward shift with an average rate of 6.1 m per decade was estimated for the Northern Hemisphere in the course of present century (Parmesan and Yohe, 2003). But the response of treeline to climate warming has been mixed, with some treelines showing evidence of recruitment at higher altitudes and/or latitudes (advance) whereas other reveal no marked change in the upper limit of tree establishment (Harsch et al., 2009). In fact, treelines are not always keeping pace with climate change on decades to millennia scales. The species competition during the recruitment phase may temper effects of climate warming on a time scale of decades (Liang et al.,

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2016). Abiotic factors, such as permafrost persistence and distant glacial refugia, may lead to the vegetation-climate disequilibrium on a time scale of millennia (Herzschuh et al., 2016).

Biodiversity has been widely suggested to have great impacts on stabilizing ecosystem process and depend strongly on the degree of change in climate variables (Chen et al., 2011; Kreft and Jetz, 2007; Pauli et al., 2012). Climate changes in the past have had dramatic repercussions, and these have certainly resulted in extinctions and extensive shifts in species ranges (Chen et al., 2011; Lovejoy and Hannah, 2005). Treeline ecotones have high plant diversity, compared to the forest at lower elevation and the treeless tundra at high elevation (Hofgaard and Wilmann, 2002). But the biodiversity changes in treeline ecotone are complicated, due to direct climate pressure as well as the vegetation belts shift and species competition (Norberg et al., 2012; Wielgolaski et al., 2017). Recent (2001–2008) changes in vascular plant species richness revealed that species had moved upslope on average but with opposite effects on the summit floras' species richness in boreal-temperate mountain regions (+3.9 species on average) and Mediterranean mountain regions (−1.4 species on average) (Pauli et al., 2012). Despite the fact that scientists have contributed a great deal of effort to reveal the potential mechanisms about climate-induced changes in plant species migration and plant diversity, it is still insufficient to gain a comprehensive understanding about these processes due to the lack of long-term and large-spatial observational data or high-resolution records (Chen et al., 2011; Seddon et al., 2014; Wielgolaski et al., 2017). In addition, it is still unclear in what extent climate change and treeline shift drive the biodiversity change in treeline ecotone.

Southeastern Tibetan Plateau (TP) has the highest treeline, consisting of *Juniperus tibetica* at 4900 m a.s.l., in the Northern Hemisphere (Miehe et al., 2007) and is very sensitive to global climate change (D.L. Chen et al., 2015). Recent studies show that climate warming tends to promote an upward shift of alpine treeline on the southern and eastern TP (Baker and Moseley, 2007; Gaire et al., 2017; Kramer et al., 2010), although the upslope migration rates of alpine treeline are controlled by local factors such as microsite availability and interspecific interactions on a timescale of decades (Liang et al., 2016; Wang et al., 2012). On the centennial to orbital timescales, vegetation belts moved up and down along with climate oscillations have been reported (Herzschuh et al., 2006; Li et al., 2011). Therefore, some of these treelines free from direct human disturbances are suitable to investigate the treeline positions and biodiversity changes under variable climate conditions over a long-term period.

As an important proxy for studying past vegetation changes (Nolan et al., 2018; Zhao et al., 2015) and their associated plant richness and diversity over long time scales (Birks et al., 2016b; Birks and Line, 1992; Felde et al., 2015; Odgaard, 1999), palynological data provides pivotal information about shifts of vegetation belt (Herzschuh et al., 2006; Li et al., 2011; Pellatt and Mathewes, 1997), plant and landscape diversity (Berglund et al., 2008; Birks et al., 2016a; Felde et al., 2015), and non-linear responses, time lags, stability and resilience of ecosystems to human land use and climate change (Berglund et al., 2008; Herzschuh et al., 2016; Miras et al., 2015). Former palynological studies on the TP were mainly focused on the glacial-interglacial scales and the Holocene, but limited by chronological control and temporal resolution with respect to the past millennium. Recently, we have reported an archive of lacustrine sediment from Basomtso on the southeastern TP, with averaged deposition rate of ~0.5 cm/yr (Li et al., 2017). Thus, the palynological data from Basomtso record may provide high resolution and long-term biotic response to climate change over the past millennium.

Herein we present the results of fossil pollen record from Basomtso. Our aim is to analyze treeline composition and biodiversity change over the past millennium, and provide insights to recent alpine vegetation change on the southeastern TP. This article focuses on the following questions: (i) How did the treeline position and plant diversity on the southeastern TP change over the past millennium? (ii) How did changes in these processes relate to climate change in centennial scale? (iii) How did treeline ecotone work as a junction for vegetation composition, treeline position and plant diversity?

1.1. Regional setting

Basomtso (93°53′42"~94°1′48″ E, 30°0′0"~30°2′55″ N, 3476 m a.s.l.) is located in the eastern Nyainqentanglha Mountain on the southeastern TP (Fig. 1a). The lake is surrounded by mountains with an altitude of 4500–5200 m a.s.l. and slope angles of 45–55° (Fig. 1b). Modern temperate glaciers distribute in the basin, and main peaks above 5500 m are covered by permanent ice caps (Fig. 1b). Climate on the southeastern TP is dominated by the Indian Summer Monsoon, characterized by relatively warm and wet summers and cold and dry winters. Climate information from local weather station (94°28′1.2″ E, 29°34′1.2″ N, at 3001 m a.s.l., ~65 km to Basomtso) in Nyingchi yields a mean annual temperature of 9 °C and a mean annual precipitation of 1130 mm. According to a lapse rate of 0.55 °C per 100 m, the mean annual temperature at Basomtso should be ~6.4 °C, with a mean July temperature of ~13.3 °C, and a mean January of approximate −1.7 °C. The lake is ice-free in winter.

Altitudinally-controlled vegetation belts occur in the south slope of the eastern Nyainqentanglha Range (Li et al., 1985). The mixed broadleaf-conifer forest can be found between 2500 and 3200 m a.s.l., comprising primarily *Pinus* and *Quercus*. The vegetation around Basomtso is alpine coniferous forest comprising *Picea* and *Abies*, with the elevations of 3200–4200 m a.s.l. (Fig. 1c). *Picea* and *Abies* are dominated edificators and sometimes present as pure forest. The upper treeline stands at about 4200 m a.s.l., beyond which the forest gives way to alpine shrub, alpine meadow and alpine tundra with increasing altitude. Alpine evergreen coniferous shrub and alpine meadow appear on the south and east slopes in the Basomtso basin, mainly comprising of Cupressaceae and *Kobresia*. Alpine meadow and alpine sclerophyllous evergreen broad-leaved shrubs occupy the north and west slopes, dominated by *Kobresia* and Ericaceae. The alpine sparse vegetation comprising mainly *Saussurea* dominate the high elevation above 4500 m a.s.l., and glaciers and snow cover can be found above 5200 m a.s.l. in the Basomtso basin (Fig. 1c).

Study on the treeline of Sejila Mt., about 70 km away from Basomtso, revealed that the upper limit of closed forest was located at the altitude of 4320 m, with treeline ecotones of 250-m vertical width on sunny slopes and 70-m vertical width on shady slopes, respectively (Yang, 2007). Species richness and diversities of arbors, shrubs and grasses all decreased along with the increase of altitudes from 3800 m to 4300 m α diversities of plant communities on the sunny slopes were higher than that on the shady slopes. Diversity indexes of different plant types at timberline on the sunny slope was in order of arbors < shrubs < grasses, and those on the shady slope of arbors < grasses < shrubs. The treeline ecotones on the sunny slopes have high plant diversity, compared to both plant communities at lower and higher elevations. However, on the shady slopes, it shows an opposite pattern.

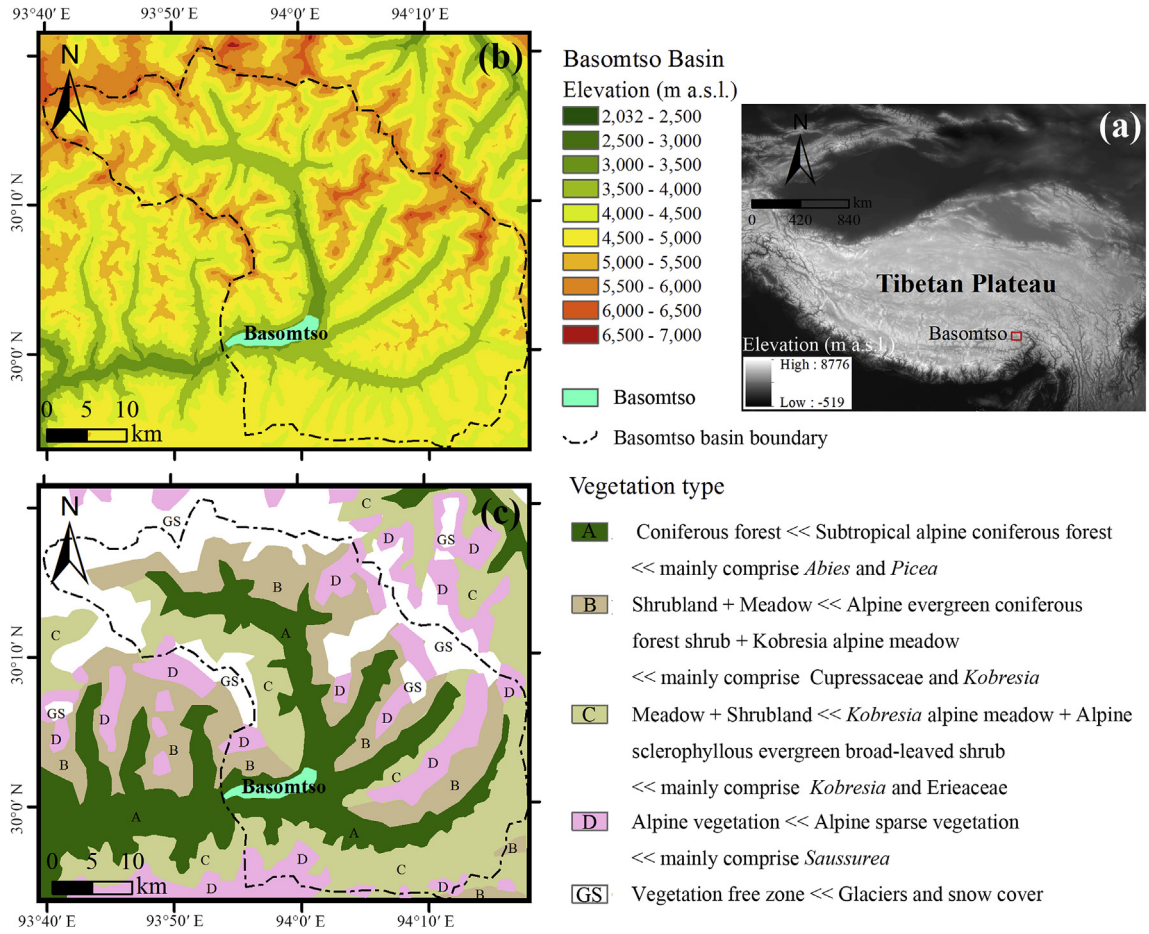

Fig. 1. Maps showing the location of Basomtso on the Tibetan Plateau (a), the elevations of Basomtso basin (b), and the vegetation types around Basomtso (c). Both the maps of (a) and (b) are created using the software of ArcGis 10.2 based on the digital elevation map downloaded from USGS (http://www.dgadv.com/srtm30). We redraw the map of (c) based on the Vegetation Atlas of China (Zhang, 2007).

2. Materials and methods

2.1. Field sampling and sediment dating

In October 2012, a 4.82-m-long sediment core (BSCW-1) was retrieved from Basomtso at a water depth of 120 m using a UWITEC sample system. The age-depth model based on six well preserved leaves has been reconstructed and further confirmed by the ^{137}Cs profile and varve counting from short sediment cores (Fig. 2). According to the age-depth model, the basal sediment was deposited from 951 to 813 cal yr BP, with a median age of 867 cal yr BP. The averaged sedimentary rate is estimated *ca.* 0.53 cm/yr during the past millennium.

2.2. Pollen analysis

A total of 120 samples for pollen analysis were treated using standard laboratory methods (Faegri et al., 1989). Samples were sequentially treated with HCl (10%) to remove carbonate, with HF (50%) to remove silicate, boiling in KOH (10%) to remove humic acid, sieving to remove the fine and coarse fractions, and then mounting in silicone oil. To calculate concentrations of pollen, tablets containing a known quantity of *Lycopodium* spores were added to each sample prior to the treatments. At least 300 terrestrial pollen and spore grains per sample were counted. Pollen percentages were calculated based on the total pollen count of arboreal and terrestrial non-arboreal taxa and were used for pollen diagram and for numerical analyses. 20-terrestrial pollen types with a representation >2% in at least five samples were included in a stratigraphically constrained cluster analysis by using CONISS program in the Tilia software (version 2.0.6, Grimm, 1993). The ratio of typical arboreal (*Abies* and *Picea*) pollen percentages to typical non-arboreal (terrestrial shrub and herb taxa) pollen percentages was calculated and presented as AP/NAP. The LOESS smooth method was introduced to highlight the main trends of this ratio.

2.3. Numerical analyses

Pollen richness can be used as a proxy of plant richness and diversity at local to landscape scales (Birks et al., 2016a; Odgaard, 1999). The series of diversity numbers presented by Hill (1973) provide a conceptually simple and mathematically rigorous basis for estimating richness, evenness and diversity (Birks et al., 2016a). *Hill* numbers of *N0*, *N1* and *N2* are three widely used measures of diversity, which give easily interpretable numbers and provide information at three different levels based on how rare and abundant taxa are weighted (Birks et al., 2016a; Chao et al., 2014). *N0* is the number of taxa in a sample regardless of their abundances, *N1* (the exponential of the widely used Shannon diversity or entropy measure) estimates the number of abundant taxa in an assemblage as it weights each taxon exactly by its relative abundance, and *N2* (the reciprocal of Simpson's diversity or concentration measure)

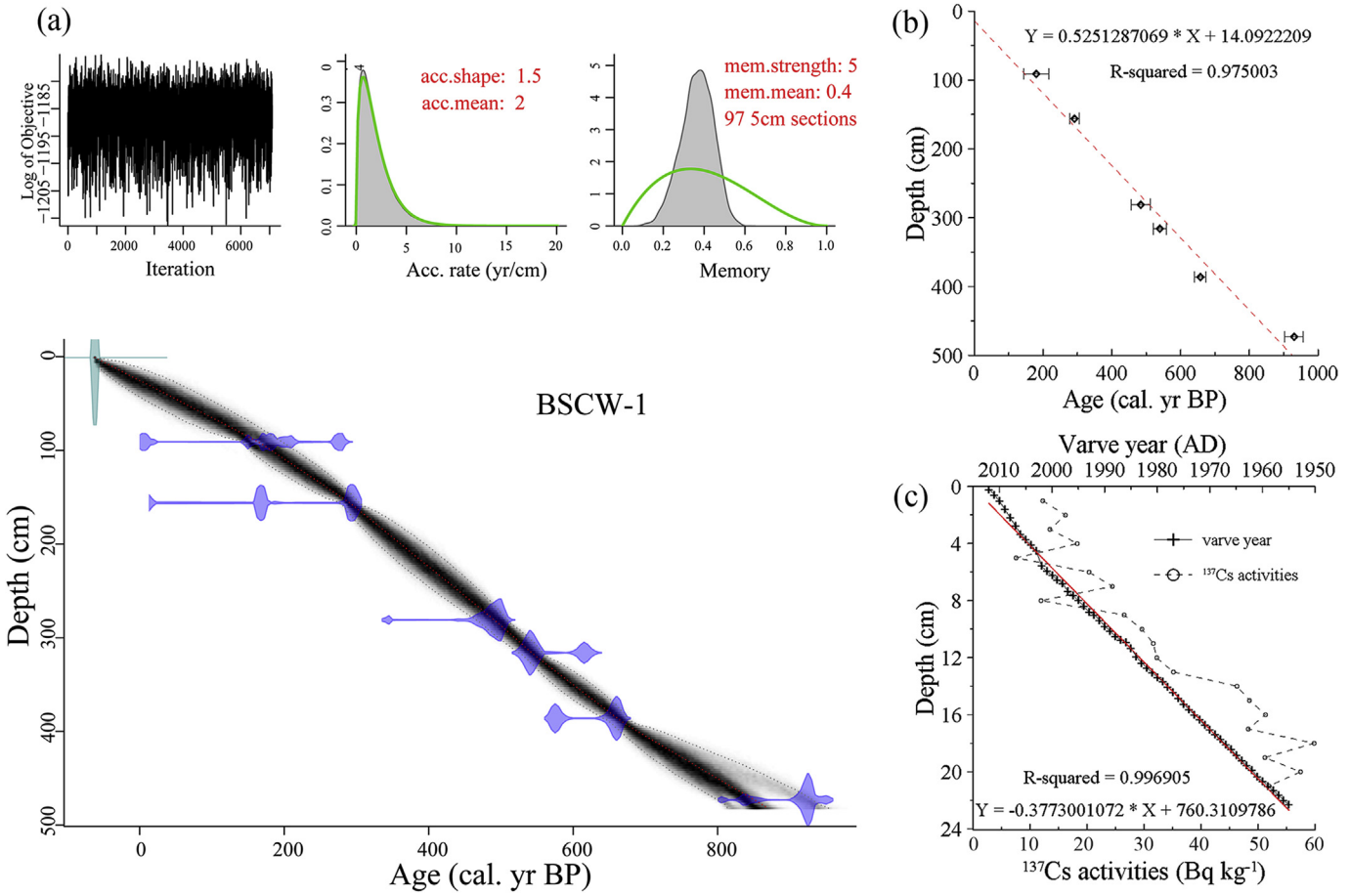

Fig. 2. Age-depth model of Basomtso core sediment (a), the depth-age relationship of the six AMS ^{14}C results (b), and the varve year and ^{137}Cs activities of a short sediment core. Detailed information referring to Li et al. (2017).

estimates the number of very abundant taxa in an assemblage (Birks et al., 2016a; Hill, 1973).

Estimates of plant richness and diversity derived from complex pollen data maybe biased in various ways, such as the count size and the pollen representation (Weng et al., 2006). Some approaches reviewed by Birks et al. (2016a) have been developed to minimize these biases, but the deep-rooted biases cannot be fully eliminated. Instructively, a former study conducted by Felde et al. (2015) manifested that the statistically significant relationships exist between untransformed pollen data and the pollen and spore equivalents in the alpine regions and that transforming of pollen abundances (e.g., the pollen representation) did not improve these relationships. It means that the use of untransformed pollen data can provide a reasonable estimation of plant richness and diversity at alpine regions. We therefore did not transform our pollen data in the calculation of *Hill* numbers and also in the explanation of our results.

To minimize the bias of differing sample size and provide 95% confidence intervals for *N0*, *N1* and *N2*, extrapolation of *Hill* numbers described by Chao et al. (2014) had been introduced. The exaggerated pollen grains had been set 1000 in the calculation. Pollen assemblage evenness had been estimated by busing *Hill* modified ratio (*N2*-1)/(*N1*-1) (Alatalo, 1981), since it is informative for the proportions of dominant taxa or common taxa (Felde et al., 2015) and is more ecologically meaningful than other evenness measurements (Birks et al., 2016a). Three measures of *Hill* numbers were calculated using function in R package 'iNEXT' (Hsieh et al., 2016).

Species Contributions to Beta Diversity (SCBD) and Local Contributions to Beta Diversity (LCBD) approaches (Legendre and De Cáceres, 2013) were used to identify the important pollen taxa (those with high SCBD indices) in structuring the montane vegetation community and estimating the ecological uniqueness of the sample unites (i.e., different time slices in this study) in community composition (LCBD indices). Five data sets were created, including complete-pollen data set, tree-pollen data set, shrub-pollen data set, herb-pollen data set and fern data set. SCBD indices was only applied to complete-pollen data set, while LCBD indices was applied to the rest data sets. LCBD and SCBD indices were calculated using function in R package 'adespatial' (Dray et al., 2018). In order to highlight the main trends between richness and diversity, the LOESS smooth method was introduced in comparing the richness, diversity estimates, SCBD and LCBD indices. All the numerical analyses were implemented in R (version 3.4.4, R Core Team, 2016).

3. Results

3.1. Pollen assemblages

116 pollen and spore types in total were identified from 120 samples. The pollen concentrations show dramatic changes over the past millennium, with relatively low levels during *ca.* 750-100 cal yr BP (Fig. 3). Stratigraphically constrained cluster analysis divides the pollen profile in two subzones at *ca.* 400 cal yr BP. According to the averaged pollen percentages, we divided all the pollen taxa recognized from Basomtso sequence into three classes,

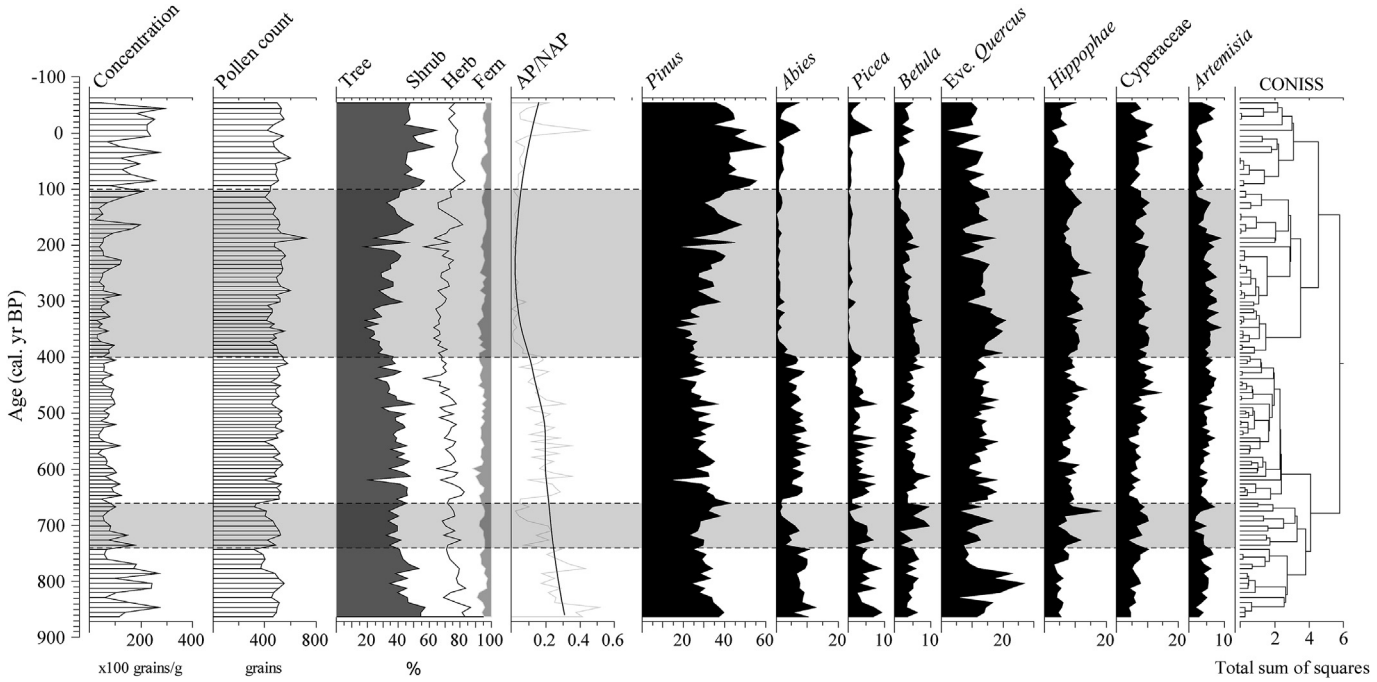

Fig. 3. Pollen diagram of the dominant taxa with averaged percentage higher than 2%, and the pollen sum, pollen compositions and concentrations. AP/NAP is the ratio of *Picea* and *Abies* to that of terrestrial shrub and herb taxa, with the black line representing the result of LOESS smooth.

i.e., the dominant pollen taxa, the common pollen taxa and the rare pollen taxa.

The dominant pollen taxa are the species with averaged pollen percentages higher than 2%, including *Pinus*, *Picea*, *Abies*, evergreen *Quercus* (eve. *Quercus*), *Betula*, *Hippophae*, *Artemisia* and Cyperaceae (Fig. 3). Most of those 8 pollen taxa are edificators and/or dominant species in different vegetation types on the southeastern TP, whose variations are ecologically meaningful. The most outstanding feature of the dominant taxa is the gradually decreases in *Pinus, Picea* and *Abies* and the increases in *Betula*, eve. *Quercus*, *Hippophae*, *Artemisia* and Cyperaceae before *ca.* 400 cal yr BP, after which both the *Picea* and *Abies* were almost absent. Since *ca.* 100 cal yr BP, the pollen grains of *Picea, Abies* and *Betula* turned to increase, along with the decreases of eve. *Quercus*, *Hippophae*, *Artemisia* and Cyperaceae.

A total of 17 common pollen taxa with averaged percentages between 0.5% and 2% can be found in Fig. S1, such as Cupressaceae/Taxodiaceae, *Carpinus*, *Salix*, Ericaceae, *Alnus*, deciduous *Quercus* (dec. *Quercus*), Gramineae, *Polygonum*, Ranunculaceae, *Polypodium*, and *Athyrium*. These common taxa are generally dominant or accompanying taxa in different vegetation types on the southeastern TP, such as Cupressaceae/Taxodiaceae in coniferous taxa, *Salix* and Ericaceae in shrub taxa, Ranunculaceae in herb taxa, and *Polypodium* in fern taxa. Comparing with dominant pollen taxa, the variations of common pollen taxa are with minor amplitude. Pollen of *Salix*, Ericaceae, Ranunculaceae and Labiatae showed obviously increase after *ca.* 400 cal yr BP. Dec. *Quercus* was with higher pollen percentages at the onset of past millennium and then soaring during *ca.* 740-710 cal yr BP, after which it remained in a relatively low level.

A total of 91 rare pollen taxa with averaged pollen percentages below 0.5% have been recognized (Fig. S2), such as *Clematis*, *Spiraea*, Solanaceae and Liliaceae. Those taxa are generally accompanying species and/or occasional species in the alpine regions on the southeastern TP, whose significances in vegetation are subordinate in maintaining the community structure and function. However, they are fundamental for the vegetal biodiversity.

3.2. Treeline movements

Modern vegetation above the Basomtso changes from alpine coniferous forest to alpine shrub, and finally to alpine meadow and tundra with increasing altitude. If the treeline shifts downward to the lakeshore, the shrunken coniferous forest and expanded shrub-meadow areas were expected to input less *Abies* and *Picea* pollen but more shrub and herb taxa pollen. On the contrary, when vegetation belts move upwards with coniferous forest expanding, the lower limit of alpine shrub and meadow was expected to shift upper slopes far away from the lakeshore, causing an increase of *Abies* and *Picea* pollen but a reduction of shrub and herb pollen in lake sediment. Although the pollen production and preservation processes are influenced by factors on multi-annual time scales, the changes of coniferous taxa pollen to that of shrub and herb taxa should be closely related to the vegetal distribution patterns on multi-decadal to multi-centennial time scales. The LOESS-smoothing AP/NAP can therefore provide the vital information about the shift of altitudinal vegetation belts surrounding the Basomtso.

During the period of *ca.* 867-600 cal yr BP, coniferous forest treeline slowly shifted downward, after which the treeline remained stable for about 100 years (Fig. 3). After *ca.* 500 cal yr BP, treeline shifted downward remarkably. The alpine coniferous forest shrunk rapidly as the *Abies* and *Picea* was reduced. The pollen abundances of some shrub and herb taxa such as *Betula*, eve. *Quercus*, *Hippophae*, *Artemisia*, Rosaceae and *Thalictrum* increased at the beginning of this period and then deceased as well. The lowest treeline for the past millennium occurred in the period of *ca.* 260-200 cal yr BP. An increase trend of treeline was recorded after *ca.* 200 cal yr BP.

3.3. Variations of Hill numbers and diversity index

The results of *Hill* numbers *N0*, *N1* and *N2* have been shown in Fig. 4. *N0* fluctuated during *ca.* 867-400 cal yr BP. Remarkably increases of *N0* had been recorded at *ca.* 450 cal yr BP, and high values

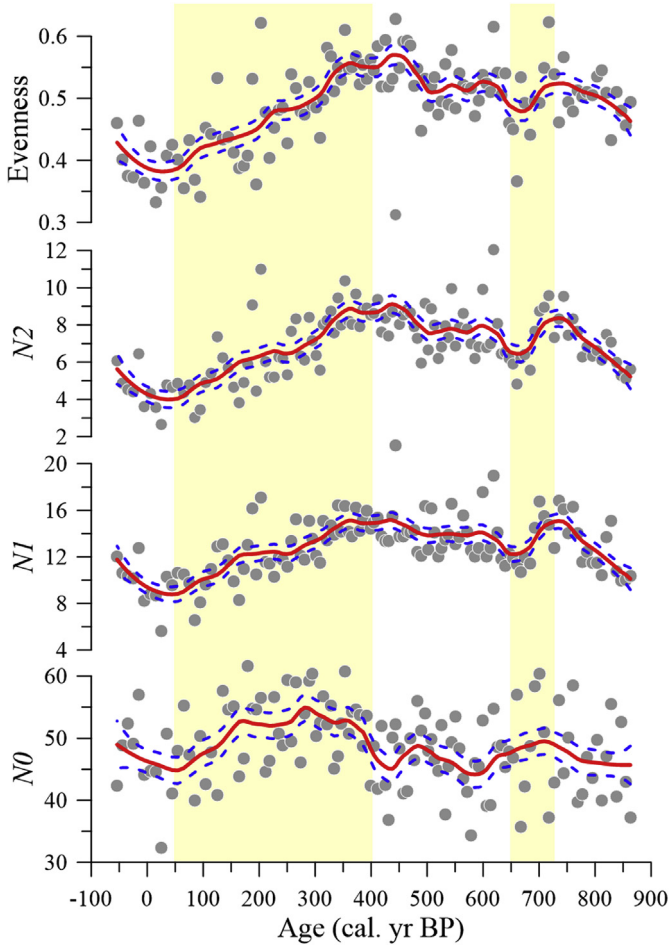

Fig. 4. Variations of *Hill* numbers and the evenness estimate. The red solid lines are loess smoothing curves, blue dash lines represent standard errors, yellow shadows indicate two cold episodes mentioned in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of *N0* are obvious during *ca.* 400-150 cal yr BP. Decreasing trend of *N0* was outstanding from *ca.* 150 to *ca.* 50 cal yr BP, after which a slight increase trend was obvious.

N1 and *N2* showed similar tendencies. For the period of *ca.* 867-720 cal yr BP, both *N1* and *N2* increased rapidly to high levels. This period was followed by a sudden and distinct decrease in them. Both *N1* and *N2* recovered gradually to another high value at *ca.* 350 cal yr BP. Considerable declines happened during *ca.* 350-50 cal yr BP. This situation was reversed slightly over the recent decades.

The variations of evenness index were basically similar to that of *N1* and *N2*, with increase trends before *ca.* 720 cal yr BP and during *ca.* 650-480 cal yr BP, as well as decrease trends during *ca.* 730-650 cal yr BP. The evenness index reached its maximum value at *ca.* 480 cal yr BP, and remained high values from *ca.* 480 to 350 cal yr BP. The evenness index decreased dramatically from *ca.* 350 to 50 cal yr BP. Slight increase of evenness index could be found after *ca.* 50 cal yr BP.

3.4. Variations of LCBD and SCBD indices

LCBD indices of tree taxa shows a roughly opposite trend with that of other taxa (Fig. 5a). A low value of LCBD-Tree indices at *ca.* 700 cal yr BP corresponded to the peaks of other LCBD indices. The most significant high level of LCBD-Tree indices occurred between *ca.* 400 and *ca.*100 cal yr BP, while the corresponding indices of other pollen type were relatively low. After *ca.* 100 cal yr BP, LCBD-Tree indices decreased rapidly with noticeable increases in the indices of other pollen types. SCBD indices show that herb (34.48%) and shrub (33.27%) contributed around 2/3 of the compositional change over the past millennium (Fig. 5b). Tree and fern accounted for 23.31% and 8.94%, respectively.

4. Discussion

4.1. Treeline dynamics

Temperature is generally considered to be the primary determinant for treeline location (Harsch et al., 2009; Körner, 1998; Paulsen and Körner, 2014), and strong and long-term climatic changes are able to produce significant changes in vegetation patterns in alpine regions (Holtmeier and Broll, 2007; Körner, 2003). Although lacking millennium-long temperature record in our study region, tree-ring data from the mid-eastern TP showed a fluctuated decreasing mean annual temperature during 1000-1600 CE (Liu et al., 2009). This cooling temperature was also consistent with the summer temperature reconstruction from the extra-tropical Northern Hemisphere which was characterized by warm anomalies during 1350–1450 CE and cold anomalies representing the culmination of the Little Ice Age (LIA) in the 17th century (Christiansen and Ljungqvist, 2012). It is worth noting that the long-term trends of treeline record (LOESS-smoothing AP/NAP) from Basomtso was synchronous with the temperature anomalies (Fig. 6). The coldest period of the past millennium occurred during *ca.* 400-100 cal yr BP on the southeastern TP (Zhu et al., 2011), with regional glacial maximum caused by reduced temperature in the 17th century (Loibl et al., 2015). Consistency between patterns of treeline shifting and centennial-scale temperature change implies temperature as a key factor controlling the direction of treeline shifting in the study region. A persistent warmer condition will trigger treeline moving upward while cooler condition will lead to downslope movement.

A pronounced warming trend is apparent across the southeastern TP (Liang et al., 2009; Liu et al., 2009; Zhu et al., 2011), which is expected to shift treelines upward with an average shift rate of 2.9 m per decade (range: 0–8.0 m per decade) (Liang et al., 2016). The increasing trends of growing season (summer) temperature had been recorded on the southeastern TP since the mid-17th century (Liang et al., 2009; Zhu et al., 2011). The reconstructed treeline locations, at 50-yr intervals on the southeastern TP using standard dendrochronological methods, indicated that the current treeline has upward shifted about 56.5 m (range: 2.7–114.3 m) since the mid-17th century (Liang et al., 2016). In our record, the increase in the LOESS-smoothing AP/NAP also indicates an upward shift of the treeline since the mid-17th century (Fig. 6). Modern treeline position stands at 4200 m a.s.l. around Basomtso region. Given that the averaged shift rate of 2.9 m per decade was stable during the warming phase, we could reach the conservative estimation of the treeline position at 4127 m a.s.l. around the Basomtso region during the culmination of the LIA in the mid-17th century. But our estimation is with uncertainty and needs further verification by other methods, especially the plot-based dendroecological reconstructions. In addition, we still have no idea about the exact treeline position during the cooling phase, i.e., before the 17th century, because of lacking information relating to the downward shift of treelines. But we suggest that the older treeline position before the 14th century was higher than the modern treeline position at 4200 m a.s.l., based on the variations of LOESS-smoothing AP/NAP from Basomtso record.

Despite the broad-scale constraints on treeline imposed by

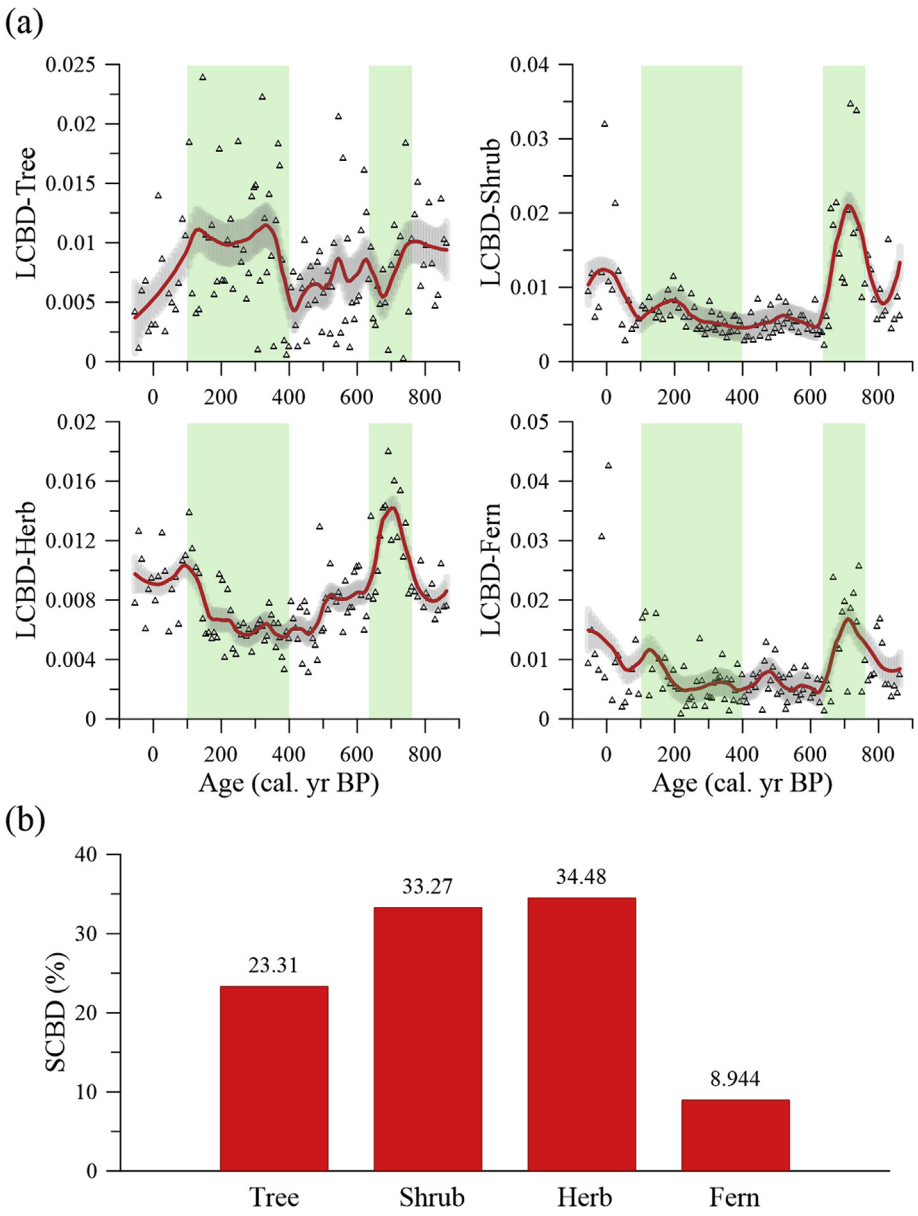

Fig. 5. LCBD indices (a) and SCBD indices (b) of different type of pollen taxa (tree, shrub, herb and fern). The red solid lines are loess smoothing curves, grey shadows represent standard errors, green shadows indicate two cold episodes mentioned in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

global-scale thermal trends, factors other than temperature influence treeline elevation and structure at fine spatial scales (Daniels and Veblen, 2004; Körner, 1998; Liang et al., 2016; Wang et al., 2012). Regional to local scale factors are particularly important in mountainous terrain, where topographic effects modify coarse-scale climate trends (Luckman and Kavanagh, 1998). Southeastern TP includes mountains and valleys along the middle reaches of the Brahmaputra River, through which the humid Indian Summer Monsoon penetrates into this corner of the Plateau and brings moisture to support dense forest vegetation growing on the valley slopes (Chang, 1981). Summer season (June to August) moisture reconstruction from Xinpu, about 40 km away from Basomtso basin, indicates above average humidity conditions during the LIA and below average humidity conditions since the 1850s (Wernicke et al., 2015). This pattern has been revealed by several other tree-ring records from the southeastern TP as well, although they show some local differences (Bräuning and Mantwill, 2004; Grießinger et al., 2011; Wernicke et al., 2017). Therefore, treeline shifting downward during wetter episode either backs up the idea that temperature is the major limitation for treeline shifting in Basomtso region, or suggests a negative effect of humid climate on spruce/fir forest decline. Despite lacking information about the negative effect of water stress on plant physiology in the study region, limited increases in humidity or precipitation (~5% relative humidity and ~50-mm precipitation) during *ca.* 400-100 cal yr BP may hardly result in significant forest decline in this relative humid area (Fig. 6). In addition, although soil moisture seems to be sufficient, root activity can be constrained by low-temperature, which further depress the ability for plants to acquire water from cold soil (Körner, 1998). It is interesting that treeline around Basomtso did not rise above the highest level of the past millennium during the Modern Warm Period. Some studies suggest that temperature-

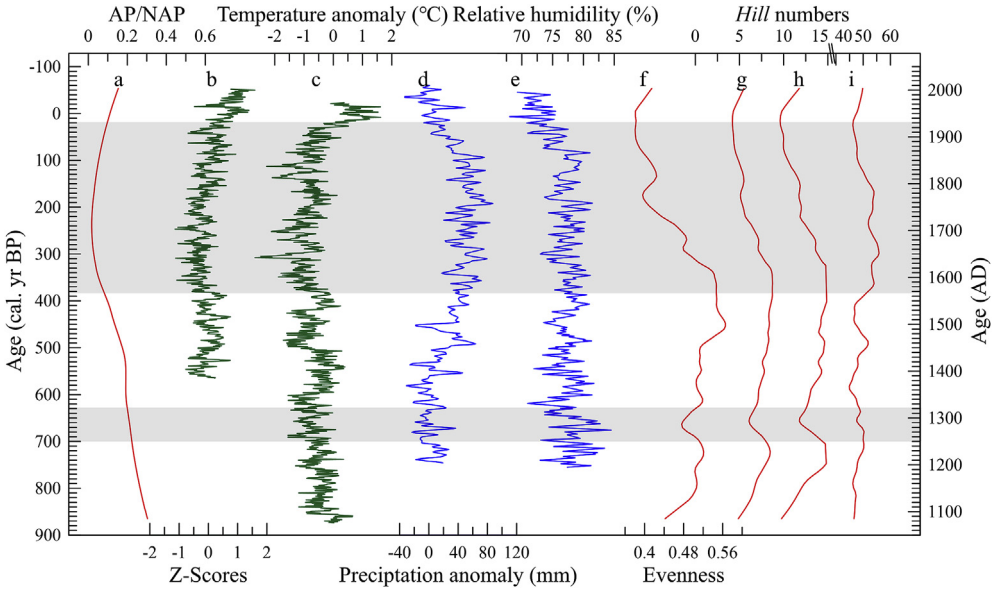

Fig. 6. Comparisons of the LOESS-smoothing AP/NAP, evenness index, LOESS-smoothing *Hill* numbers with the temperature and humidity/precipitation reconstructions from the southeastern TP and the Northern Hemisphere. **a**, AP/NAP. **b**, August temperature reconstruction on the southeastern TP (Zhu et al., 2011). **c**, low-frequency temperature variability from the extra-tropical Northern Hemisphere (Christiansen and Ljungqvist, 2012). **d**, August precipitation reconstruction at Reting (Grießinger et al., 2011). **e**, summer relative humidity reconstruction at Xinpu (Wernicke et al., 2017). **f**, evenness index. **g**, *N0*. **h**, *N1*. **i**, *N2*.

induced drought stress is reducing growth of boreal forest trees, which may have spread to cooler and moister sites (Lloyd and Fastie, 2002). Therefore, the most likely conclusion has to be that moisture decline combined with temperature increase may have restricted significant upshift migration of treeline in Basomtso region, but long-term observation and detailed studies on plant physiology are essential to reach a final conclusion.

Snow and glacier may also attribute to treeline shifting around Basomtso. Climate warming has caused substantial glacial retreat on the southeastern TP (Loibl et al., 2015). The growth limitation hypothesis suggests that cold soil severely constrain the growth and activity of roots (Tranquillini, 2012), which has been verified by several experiments (Bengough et al., 2006; Nagelmüller et al., 2017). Cold snow/glacial meltwater infiltrates into the soil, offsetting the effect of climate warming on soil temperature and preventing or weakening the potential for seedling recruitment and forest expansion. In addition to snow/glacial meltwater, topography of deeply incised valley is another potential impact on treeline distribution in the study region. Since many large valley glaciers distributing on the southeastern TP, climate cooling will cause glaciers extending to lower altitude via the valleys. Glaciers near Basomtso reached their maximum down-valley extent during the LIA maximum, with low glacier tongue altitudes at ~3200 m (Loibl et al., 2015). The extended glacier tongues and forelands must have occupied forest habitats in the upper valleys and consequently reshaped the treeline.

4.2. Plant diversity dynamics

The crucial role of disturbances in maintaining biotic diversity has been widely accepted (Connell, 1978; White and Jentsch, 2001). Due to natural and anthropogenic disturbances, ecosystems undergo changes that are sudden or gradual, dramatic or subtle (Sheil and Burslem, 2003; White and Jentsch, 2001). The intermediate disturbance hypothesis holds that in many communities, major disturbances occur frequently enough that succession will usually be cut short and started all over again (Connell and Slatyer, 1977). Disturbance is usually considered as a rapid release or reallocation of 'community resources' (Connell, 1978), despite definitions do vary in terms of distribution, timing, intensity, spatial and temporal variations, etc. (White and Jentsch, 2001). A unimodal (rise and fall) pattern can be used to explain relationship between species diversity and recorded range of disturbance, i.e., low and high disturbance levels allow dominance of few species, whereas intermediate disturbances increase species evenness (Connell, 1978; Sheil and Burslem, 2003). Based on this point of view, the increases of (very) abundant taxa and evenness during *ca.* 867-720 cal yr BP reflects the succession was getting closer to the 'Climax' stage. The following sharp declines from *ca.* 720 to 650 cal yr BP imply the occurrences of distinct and strong disturbances, cutting off the previous process and forcing the succession to restart. Then, from *ca.* 650 to 350 cal yr BP, the succession developed again from younger successional stage. Another major disturbance occurred and during *ca.* 350-50 cal yr BP. However, unlike a quick rebound showing after the disturbance at *ca.* 720-650 cal yr BP, (very) abundant taxa and evenness kept declining till *ca.* 50 cal yr BP. In Connell's scheme, after a severe disturbance, there is usually a burst of regeneration that, once established, suppresses later regeneration (Connell and Slatyer, 1977). Therefore, failure in regeneration during *ca.* 350-50 cal yr BP implies intermediate disturbances exist persistently over this period. After *ca.* 50 cal yr BP, this disturbance was fading, and the succession began to develop again.

Ecosystems are influenced by disturbances of various kinds, no matter they are anthropogenic or natural induced, biotic or abiotic related (Birks et al., 2016a; Colombaroli et al., 2010; Connell and Slatyer, 1977; Hampe and Petit, 2005; Miras et al., 2015). In generally, ecosystems in regions affected by very limited human activities, just as that in Basomtso area, can be considered to be impacted primarily by climate. Climate change will contribute to alterations in disturbance regime, e.g., changes of fire frequency and soil thermal regime due to variations in weather conditions (Carcaillet et al., 2001; Euskirchen et al., 2006; Flannigan et al., 2009), or an increased flooding intensity due to altered precipitation patterns (Trenberth, 2011). Fire activity research on the southern and southeastern TP are rare. Kaiser et al. (2009) did find evidence of fire activity in southern Tibet during the late Holocene

but it was related to forest clearance. While in Naleng region (southeastern Tibet), charcoal analysis excluded fires as major reason for the forest retreat since the Pleistocene-Holocene transition (Kramer et al., 2010). In addition to these evidences, subhumid climate indicated by tree-ring based reconstructions for the past 600 years (Wang et al., 2014; Wernicke et al., 2015) suggested little impact of natural fires on vegetation ecosystem on the southeastern TP.

According to the 'water-energy dynamics hypothesis', species richness (diversity) at high latitude is controlled by the availability of ambient heat, whereas, in the thermally suitable tropics, water and humidity related variables are the main driving factors (Currie et al., 2004; Field et al., 2005; Hawkins et al., 2003; Kreft and Jetz, 2007). Although the southeastern TP is not located at high latitude, the very high altitude and sufficient precipitation determine thermal stress as the main limitation for plant diversity. Therefore, the brief disturbance around *ca*.720 cal yr BP and the long-standing one during *ca.* 350-50 cal yr BP should be related to substantial change in temperature. In spite of lacking quantitative climate reconstruction before 1400 CE on the southeastern TP, an abrupt cold event around *ca.* 700 cal yr BP had been widely reported in the Tibetan records (e.g., Liu et al., 2009; Liu et al., 2014). Additionally, a sharp decrease in pollen concentration combining with changes in the composition (decreases in *Picea*, *Abies*, eve. *Quercus* and increases in *Hippophae*, dec. *Quercus* and herb taxa) in the Basomtso sediments during this interval reflects a cold climate as well (Fig. 3). For the past millennium, the most prevailing cold period (LIA maximum) occurred during *ca.* 400-100 cal yr BP (Loibl et al., 2015; Wang et al., 2014; Zhu et al., 2011). The multi-centennial cold event worked as a persistent disturbance and thus hindered the development of vegetation succession. Whereas, along with the end of LIA and substantial increase in temperature, our data reveal only a small progress in the succession since *ca.* 50 cal yr BP (Fig. 4). It is widely acknowledged that, as the long-life span of many tree species and the resilience of established forest communities to environmental changes, temporal separation between climate and plant diversity is to be anticipated (Körner, 1998).

LCBD indices of different pollen types reveal their contributions to the community composition over the past millenium (Fig. 5a). During *ca.* 780-680 cal yr BP and since *ca.* 100 cal yr BP, non-arboreal taxa were the main contributors to the compositional variations. It was not until *ca.* 400 cal yr BP that the arboreal taxa became the most important contributors. Comparing with arboreal species, non-arboreal species have shorter life span and thus can response more rapidly to the briefly cold episode and recent climate warming. Temperature in the study region had been decreasing several hundred years before arboreal species changing noticeably, which suggests that responses of tree species lag behind the climate change on the southeastern TP. Since glaciers distribute in higher mountains of the Basomtso region, temperature increase could have been smaller or less significant due to reduced cryospheric feedback (You et al., 2010). Additionally, the thermal mosaics of alpine landscapes create fine-scale habitats that are inhabited by species with different thermal preferences and therefore buffer alpine plant diversity against climate warming (Scherrer and Körner, 2011). The combined effects of plant ecophysiology, local climate and landscape may be responsible for the slow development of vegetation succession in the early stage of climate warming.

4.3. Potential links between treeline movement, composition and diversity

Vegetation changes along spatial gradients consist of changes in both quantity (diversity) and quality (structural composition; e.g., occurrence of tree-forming species and their physiognomic stature) (Hofgaard and Wilmann, 2002). Treeline ecotone, defined as the transition from the timberline to the treeless alpine vegetation (Körner, 2003), involves changes of life forms (from trees to herbs) and is characterized by many plants that are located at the limit of their ecological distribution range (Becker et al., 2007; Wielgolaski et al., 2017). Since treeline ecotone plays a crucial role in modifying the flows of material across the landscape and in regulating ecosystem and landscape processes, spatial or temporal rates of change in ecological structure or function in these zones are rapid relative to rates across the landscape as a whole (Risser, 1993). Therefore, treeline movement and changes of plant composition and diversity will be conspicuous in treeline ecotone when considerable disturbances occur.

Human activity plays an important disturbance that can strongly impact the species composition and diversity in the treeline ecotone (Colombaroli et al., 2010; Wielgolaski et al., 2017). Permanent human occupation on the TP can be traced back to 3600 cal yr BP (F.H. Chen et al., 2015). *Pinus* is considered a pioneer species after deforestation. Suppose that timber demand and deforestation were increasing with population expansion and agriculture development. The *Pinus* pollen should increase persistently over the past millennium, which is not consistent with the pollen record from Basomtso (Fig. 3). Intense timber harvesting from low-elevation forest around the lake is expected to have noticeable effect on fern community (which grows in moist shady woodland nooks in our study region). However, the percentage of fern pollen changed slightly over time (Fig. 3) and SCBD indices reveals their contribution to the pollen compositional variations is only 9% (Fig. 5b). *Stipa*, *Potentilla*, *Rumex*, *Sanguisorba*, *Apiaceae* and Chenopodiaceae had been demonstrated to be human-indicator taxa on the southeastern TP (Wischnewski et al., 2014 and reference therein). From our record, no obvious increase in the sum of human-indicator taxa can be detected. Given the above, it is reasonable to conclude that, over the past millennium, human activities have limited effect on treeline movement and plant diversity in Basomtso region.

As we mentioned in subsections 4.1 and 4.2, cold events (e.g., LIA) are important impulses or disturbances for changes in vegetation ecosystems in the Basomtso region. Körner (1998) proposed that the lower threshold temperature for tissue growth and development appears to be higher than 3 °C and lower than 10 °C, possibly in the 5.5–7.5 °C range, most commonly associated with seasonal means of air temperature at treeline positions. The estimated average temperature around treeline position (*ca.* 4320 m a.s.l.) in Sejila Mt. is about 6 °C during summer months (Ren et al., 2007). Temperature, lower than this threshold, will probably cause heat-loss stress of trees, which may lead to tree mortality around the treeline.

A general cooling trend of global ocean surface temperature and terrestrial temperature during 1000–1800 CE has been verified (Christiansen and Ljungqvist, 2012; Mcgregor et al., 2015). The reconstruction of August minimum temperature anomalies in the Bomi-Nyingchi area, manifested lower temperatures, about 1.0 °C below than present, in the 1380s and 1430s, followed by a warmer period until the 1580s (Zhu et al., 2011). We assume that this climatic condition should have hindered the growth of coniferous taxa to a certain extent but facilitated the growth of shrub and herb taxa in the treeline ecotone. This assumption is further verified by the variations of pollen assemblage, with gradually decreases of *Picea* and *Abies*, and basically increases of shrub and herb taxa such as *Hippophae*, *Artemisia* and Cyperaceae (Fig. 3). At the same time, the lack of long-term and high disturbance allowed the succession developing to the 'Climax' stage in the treeline ecotone, characterized by increased of (very) abundant taxa and evenness (Fig. 4).

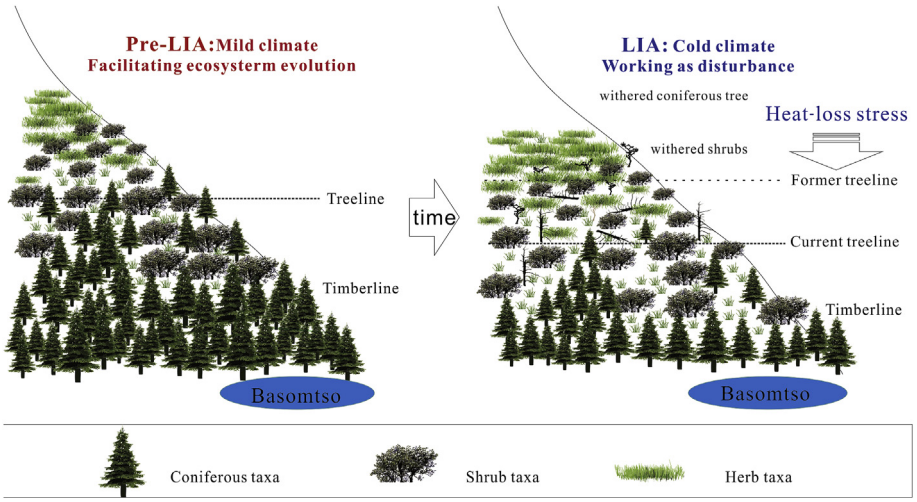

Fig. 7. Conceptual model of treeline ecotone as a tie-point for treeline movement and plant diversity changes in the alpine regions above Basomtso. The mild climate preceding the LIA facilitated the vegetation succession and the cold climate during the LIA hindered the development of vegetation succession. The chilly weather during the LIA leading heat-loss stress of trees, should have caused tree mortality in the treeline ecotone, and finally contributed to the downslope shift of treeline and to the change of plant diversity.

LIA maximum on the southeastern TP occurred during *ca*. 400-100 cal yr BP (Loibl et al., 2015; Wang et al., 2014; Zhu et al., 2011). The averaged August temperature dropped more than 1 °C during 1580–1600 CE (Zhu et al., 2011). The dramatically decreased temperature should give rise to the severe heat-loss stress in the treeline ecotone, leading to treeline shifting downslope along with the ecotone in the mountains above the Basomtso (Fig. 7). The population of dominant tree species, such as *Picea* and *Abies*, decreased significantly (Fig. 3). Meanwhile, cold-tolerated species was expanding into the previous ecotone and even invading into the 'gap' where the forest had retreated from (Fig. 3). In addition, treeline retreat created open spaces in which the expanding of rare and/or new species can colonize, which subsequently promoting species richness in a short period (Fig. 6). As the disturbance of cold climate sustaining, the cold-tolerated species will eventually outweigh the competition and replace some of the former (very) abundant species, which finally lead to a loss of diversity and evenness in the treeline ecotone (Figs. 6 and 7).

It is noticeable that the recovery of treeline and plant biodiversity fail to meet the climate warming after the LIA (Fig. 6). The fact is that the vegetation-climate disequilibrium exist (Chen et al., 2011; Herzschuh et al., 2016). Factors other than temperature, such as precipitation, glacier, and topography, modify coarse scale climate trends and/or soil hydrothermal regime on the southeastern TP, which may have locally caused the lag response of treeline distribution and plant diversity to the climate change. We therefore suggest that vegetation succession in the mountains of the southeastern TP will probably still develop slowly in the coming decades. And long-term climate, soil and vegetation monitoring and analysis are needed in order to better understand the regional dynamics of treeline movement and plant diversity change during climate transition period.

5. Conclusions

A well-dated high-resolution palynological record from Basomtso manifests the treeline movement and plant diversity change on the southeastern TP over the past millennium. Variations in the LOESS-smoothing AP/NAP suggested a basically downslope treeline movement during *ca*. 867-400 cal yr BP. At the same time, the numbers of taxa, abundant taxa and very abundant taxa as well as the evenness estimates increased. We suggest that the mild climate preceding the LIA led to the changes of vegetal composition and facilitated the vegetation succession in the treeline ecotone. Significantly downslope treeline movement and decreases of (very) abundant taxa and evenness during the cold episodes (*ca*. 350-50 cal yr BP) have been revealed, whiles the number of taxa was increased. Cooling temperature limited the growth of trees on the upper bounds of previous existing forest and thus triggered the treeline shifting downslope. Meanwhile, the cold events worked as natural disturbances cutting off the vegetation succession and forced the succession to restart, which led to the changes in the plant diversity. The resistance of trees to climate change on the southeastern TP has been demonstrated in this study. Abiotic factors should be responsible for this lag response of treeline distribution and plant diversity to the climate warming. In this case, more efforts are needed to take systematic investigation on the vegetation-climate relationships on the southeastern TP at broad spatial and temporal scales.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2018.12.029.

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